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Using Key Biodiversity Areas to guide effective expansion of the global protected area network

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Abstract

Using spatial prioritization, we identify priority areas for the expansion of the global protected area network. We identify a set of unprotected key biodiversity areas (KBAs) that would efficiently complement the current protected area network in terms of coverage of ranges of terrestrial vertebrates. We show that protecting a small fraction (0.36%) of terrestrial area within KBAs could increase conservation coverage of ranges of threatened vertebrates by on average 14.7 percentage points. We also identify areas outside both the protected area and KBA networks that would further complement the priority KBAs. These areas are likely to hold populations of species that are poorly protected or covered by KBAs, and where on-the-ground surveys might confirm suitability for KBA designation or protection.

1. Introduction

Protected areas (PA) are the cornerstone for halting the global biodiversity crisis (UNEP-CBD, 2010). While there has been a steady increase in the coverage of PAs over the last decades (UNEP-WCMC and IUCN, 2016), further expansion is needed urgently (Tittensor et al., 2014; WWF, 2016). For example, Aichi Target 11 of the Convention on Biological Diversity recommends increasing terrestrial PA coverage to 17% by 2020 (UNEP-CBD, 2010) from current 14.7% (UNEP-WCMC and IUCN, 2016). As the need to act is urgent and resources are limited, prioritization of conservation effort is important (McCarthy et al., 2012; Pouzols et al., 2014).

Global conservation priority rankings have been developed using a variety of methods ranging from simple species richness ranking (Jenkins et al., 2013) to more complex methods that, in addition to biodiversity, also account for additional factors such as costs or land-use change (Butchart et al., 2015; Pouzols et al., 2014; Venter et al., 2014). The sizes of analysis units have ranged from ecoregions down to 1 km^2 grid cells (Hoekstra et al., 2005; Myers et al., 2000; Pouzols et al., 2014). Although computation power has increased in recent years allowing finer scale analyses also at the global extent, prioritization analyses are still typically being run using rather large grids (from 10km^2 to 200 km^2)(Di Marco et al., 2017). One reason for this is the coarse resolution of globally available datasets - especially the species range maps that most of the analyses are relying on (Di Marco et al., 2017).

Global conservation prioritization analyses are needed to identify broad scale conservation priority patterns, to establish general principles about how the global PA network should be expanded, and to estimate how well it covers biodiversity (see for example Butchart et al., 2015; Pouzols et al., 2014; Venter et al., 2014). Nevertheless, the often implicitly assumed link between global conservation priorities and on the ground conservation action is not well established nor discussed widely in most the global extent prioritization analyses (see for example Butchart et al., 2015; Pouzols et al., 2014; Venter et al., 2014). In fact, country level studies have shown mixed results about whether the priority schemes affect the amount of conservation funds directed to the priority areas (Halpern et al., 2006; Holmes et al., 2012).

One reason hindering the usage of global conservation prioritization analyses to inform actual planning could be that it is hard to draw concrete suggestions for local actions based on coarse scale or vaguely delineated global priority patterns. On average PAs are much smaller than the planning units typically used in global scale conservation prioritization analyses. Usage of large grids as planning units can also lead to inefficiency in the prioritization analyses (Di Marco et al., 2017). On the other hand, inevitable lack of detail about the local circumstances in the global analyses might hinder the usage of the finer resolution global analyses to guide planning at local level.

Key Biodiversity Areas (KBA) are promoted by the IUCN as a means to identify "sites of importance for the global persistence of biodiversity" (IUCN, 2016a). KBAs are established based on clearly defined rules against which individual sites are matched (IUCN, 2016a). In contrast to global conservation priority analyses that usually consider all areas simultaneously and require spatial data across the full study area, the KBA method is applied site by site using locally available data (IUCN, 2016a). Focusing on one site at time makes it possible to use, or even collect, detailed information that is needed for delineating conservation areas in a way that accounts for e.g. local ecological processes or socio-economic reality. On the other hand, being a local, site-based approach, KBAs cannot directly account for network-level factors, such as balance between different species (complementarity) or representativeness of the network as a whole (Moilanen et al., 2009). This could potentially lead to a situation where most of the available resources are directed to areas having similar species composition, or species that might already be well covered elsewhere in the protected area network, while some other species might be completely missing.

According to IUCN standards, KBAs should be delineated so that they are manageable units, accounting for local ecological, physical and socio-economic contexts (IUCN, 2016a). These factors are important for management of any conservation areas, which makes the KBA delineation information, that is based on detailed local level information but available globally, a valuable data resource for global conservation prioritization analyses. Increasing KBA protection is generally considered to be critical to enhancing species persistence (Butchart et al., 2015, 2012). Indeed, one of the five main indicators of progress towards the Aichi target 11 is PA coverage of KBAs (UNEP-WCMC, 2017). Nevertheless, only one-fifth of the KBAs are reported to be fully protected (Butchart et al., 2015). Hence, unprotected KBAs are prime candidates for global PA network expansion (Butchart et al., 2015, 2012).

In this paper we explore the expansion of the global PA network by combining KBAs as manageable conservation units with the ability of conservation prioritization software to find globally effective solutions. Using the Zonation software (Moilanen et al. 2014), we identify global conservation priority areas for expansion of the PA network by highlighting a set of unprotected KBAs that, if protected, would area-efficiently increase mean coverage of threatened vertebrate species ranges in the global PA network while improving balance by paying highest attention to species with lowest coverage. We further identify the priority areas with most urgent need for action by considering the human influence index (HII) within priority sites. To reduce effects of uncertainty associated with range maps, we used species observations from GBIF (Global Biodiversity Information Facility, GBIF 2017) to up weight areas with confirmed sightings. By using KBAs as planning units, we aimed to reduce effects of data uncertainties and overcome some of the limitations that follow from identifying conservation priorities based on large unmanageable areas or pixels that are too small to capture ecological processes (Hurlbert & Jetz, 2007). Our view is that using KBAs as planning units can also help bridge the gap between global conservation priority analyses and site level conservation action, as KBAs are sites that could well be the focus of immediate protection. We also identify priority areas outside the PA and KBA networks that would further complement the priority KBAs. These areas are identified using a grid based analysis and thus, compared to the priority KBAs, require more information to confirm their suitability for conservation.

2. Methods

2.1. Data manipulation

We rasterized all spatial data using the intersect method, geographic coordinate system and 1 arc-minute (equal to 1.85 km at the equator) resolution. Such fine resolution was needed to approximate the location and shape of PAs and KBAs with reasonable accuracy. This raster resolution should not be confused with the size of planning units in spatial analysis, which in our main analysis was determined by the size of the unprotected KBAs. All data processing was performed with R v. 3.4.1 (R Core Team, 2017). Latitudinal variation in cell size was accounted for in Zonation analyses and data processing.

2.2. Species range maps

To identify priority KBAs, we used range maps of threatened (Critically Endangered, Endangered or Vulnerable) terrestrial mammals, birds and amphibians (n = 4,892 species) in the IUCN Red List (IUCN, 2016b). In the priority analysis of areas outside the KBA network we also accounted for Data Deficient species (n = 2,336 species). For bird species with different seasonal ranges (e.g. *Acrocephalus paludicola*, *Emberiza aureola*), we included all ranges as separate feature layers. This promotes equal coverage of all areas that are important for the survival of migratory species. Combining wintering and breeding ranges to a single input layer could lead to a situation where a species is considered to be well covered by the prioritization, but would totally lack either wintering or breeding range, potentially affecting species long term survival. Using separate input layers forces Zonation to seek balance between wintering and breeding ranges and to account for both of them in the priority areas.

2.3. Protected area and KBA data

PA data was extracted from the World Database on Protected Areas (IUCN & UNEP-WCMC, 2016) and KBA data from the World Database of Key Biodiversity Areas (KBA Partnership, 2016). We included all designated terrestrial PAs and KBAs that had polygonal representation. PAs represented only by points were discarded, because without accurate information, we thought it safer to underestimate than to overestimate PA coverage (see Visconti et al. 2013 for further discussion). The original KBA polygon data set included approximately 14,900 KBAs that were reduced to 13,700 after rasterization and removal of marine areas. Unprotected KBAs were then identified by overlaying the KBA and PA rasters. The KBA data set also included information about the criteria according to which the site was assigned the KBA status, We used this information to explore whether our prioritization method would give higher priority to KBAs that were established due to occurrence of threatened species as compared to other criteria triggering KBA definition. This could be expected because we used the range maps of threatened species as primary data in the analysis.

2.4. Species observations

Conservation prioritization analyses that use species range maps as an input data are prone to commission errors, in which species are erroneously thought to be present where it actually is not (Rondinini et al. 2006). We believe that using KBAs as planning units can reduce commission errors, because KBAs have been shown to harbor more threatened species than their surroundings (Di Marco et al. 2016). To reduce commission errors also in the analysis focusing on areas outside the KBA network, we decided to use GBIF observation as additional information about species occurrence. The rationale behind this approach is that the areas of the species ranges where the species has also been observed are also more likely to actually harbor the species. We acknowledge that this method alone does not solve the problem of false positives, but could contribute towards identifying a more robust solution.

We downloaded all GBIF observations of species with less than 5% of their range covered by the KBA and PA networks (n = 879). We only used observations that were made after 1990, because they have in general higher quality and are more informative about the present occurrence locations of the species (Ficetola et al., 2014). Because using a simple point occurrence would have given unrealistic weight for the exact position where the species were observed, we made 25 km buffers around occurrence points of each species to approximate species movement and data uncertainty. This buffer size is within typical dispersal distances for terrestrial vertebrates (Saura et al., 2018). For simplicity we decided to use only single buffering distance for all species, because the aim of the buffers was more to simply account for uncertainty in the location of the species and not to realistically model species dispersal. We intersected the buffered occurrence rasters with species ranges to remove observations outside natural ranges. We used these layers as an additional input in the priority analysis of areas outside the KBA network to upweight areas with confirmed species presences (Moilanen et al. 2006). There were 7,555 observations of 104 species (775 of the 879 species were lacking observations in GBIF) (GBIF, 2017) (Table A1, Fig. A1).

2.5. Other data

To estimate pressures from human activity to species within KBAs, we calculated mean Human Influence Index (HII, WCS and CIESIN 2005) for all unprotected sites. Human influence index has been shown to correlate with multiple factors relevant for conservation (Hand et al. 2014, Safi & Pettorelli 2010, Yackulic et al. 2011). Furthermore, we used World Bank's country income classifications for the 2019 fiscal year (World Bank, 2019) to explore how responsibility for the priority areas is divided between countries having different resources for conservation.

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2.6. Prioritization analyses

We used the Zonation v4 conservation prioritization software (Di Minin et al., 2014, Moilanen et al. 2014), to produce a global priority ranking of the unprotected KBAs for expanding the global PA network and to identify priority areas to work as candidate sites for expansion of PA network outside KBAs The analyses were run using the additive benefit function method, which aims to minimize the aggregate extinction risk over all species (Moilanen, 2007). Robustness of the results with respect to prioritization method was analyzed and confirmed, and is discussed in supplementary material (Fig A4).

Prioritization covered all terrestrial areas in a hierarchical analysis, in which highest, medium, and lowest priorities were forced into the current PA network, unprotected KBAs, and the rest of the landscape, respectively (see e.g. Pouzols et al. 2014 for hierarchic analysis). In this structure, the highest priority unprotected KBAs complement the current PA network area-efficiently in terms of balanced coverage of threatened amphibian, bird and mammal ranges. To identify priority areas for PA expansion outside the KBA network we focused on the third level of the analysis hierarchy. These areas are considered in the analysis only after species representation within the PA and KBA networks has already been accounted for and thus highest priority is given to areas that best complement the species composition of PA and KBA networks. In this third hierarchy level, each grid cell of the rasterized data was used as an individual planning unit. Zonation produces a continuous priority ranking of the full landscape (including unprotected KBAs and grid cells outside of them). In this article we focus on the highest ranking cells that would together with the priority KBA bring the PA coverage up to 17%, which is set as a target for PA coverage in the Aichi targets (UNEP-CBD, 2010). Finally, to compare the performance of the KBA based-solution to unrestricted expansion of the PA network, we did a two-level, grid-based, hierarchical analysis expanding from the present PA network to the rest of the landscape. Analysis variants are summarized in Table 1.

Table 1: *Zonation analysis variants. PAN: protected area network, PA: protected area, KBA: Key biodiversity area.*

Analysis number and name	Purpose	Data used in prioritization (planning units)	Ranking hierarchy
1) Free PAN expansion	Create a grid-cell-based PA expansion ranking to help evaluate the performance of the KBA restricted solution	Threatened species (1' grid cells)	1. PAs (highest), 2. rest of the landscape
2) Priority KBAs for PAN expansion	Rank unprotected KBAs in terms of importance for improving the representation of the study species in PAN	Threatened amphibians, birds and mammals (unprotected KBAs)	1. PAs, 2. KBAs, 3. rest of the landscape
3) Priority areas for PA expansion outside the KBAs	Identify priority areas (1' grid cells outside PAN and KBAs) for potential expansion of the KBA and PA networks	Threatened species, data deficient species, and GBIF observations of gap species (1' grid cells)	1. PAs, 2. KBAs, 3. rest of the landscape

3. Results

3.1. KBA and protected area coverage

KBAs covered 8.85% (~12 000 000 km^2) of the world's terrestrial surface. Overall, 55.8% (~6 700 000 km^2) of KBA surface area was protected, leaving 10,430 KBAs with at least some unprotected parts. Unprotected parts of the KBA network (planning units of the analysis 2 of table 1), covered approximately 3.6% (5 300 000 km^2) of the world's terrestrial surface and were spread fairly evenly, albeit with some larger gaps especially in large desert areas and the Arctic (Fig. 1A). On all continents except Oceania, the KBAs were better covered by protection than the landscape on average (Fig. 1B).

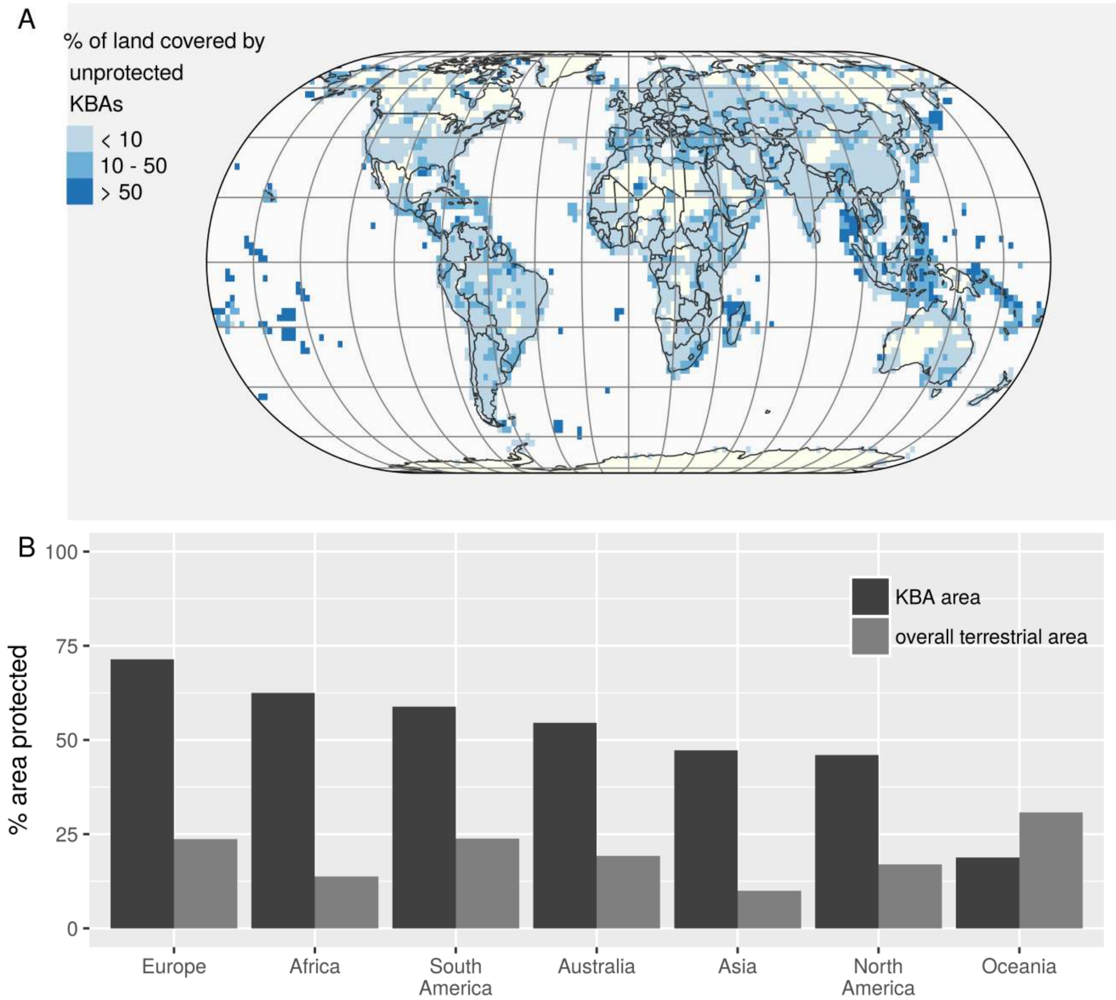

Fig. 1: Distribution of unprotected terrestrial KBAs (A) and protected area coverage of KBAs by continent (B). Panel A shows the spatial distribution of unprotected terrestrial KBAs. Darker colors indicate higher coverage of the terrestrial surface by unprotected KBAs. Terrestrial areas without any unprotected KBAs appear white. These areas cannot be reached by prioritization analysis that is limited to unprotected KBAs only. In panel B the bars show the percentage of the total KBA area that is covered by protected areas (dark gray) and overall protected area coverage of the terrestrial areas (light gray). In all continents but Oceania protected area coverage of KBAs is higher than overall protection level of terrestrial areas.

PAs covered 14.3% of the terrestrial surface with a mean coverage of 32.5% of the ranges of the study species; 302 (6.29%) species had their ranges fully protected (Table 2). However, 672 (14%) species completely lacked coverage in the PA network and these are hereafter called gap species. Together, PAs and KBAs covered 17.9% of the terrestrial surface and, on average, 54.3% of threatened species ranges, leaving only 124 (2.58%) gap species and having full coverage of 828 species ranges. As Data Deficient species are not used in the identification of KBAs, it is not surprising that the ranges of Data Deficient species are not well covered by KBAs (Table 2). In fact, 19.9% of Data Deficient species had their whole (by definition poorly known) range outside the PA and KBA networks.

Table 2: Coverage of the species ranges by different areas of interest. The number of analysis variant corresponds to the numbering in Table 1. Mean refers to mean percentage of species ranges covered. Gap species and full species refer to number of species completely missed by the solution and number of species ranges fully covered by the solution, respectively (percentage of all species in the group in parentheses). The values for"PAN and all KBAs" give the maximum species coverage that is reachable within the protected area and KBA networks. The size of the outside KBAs priority area is 2.1% of the terrestrial surface, which would together with top 10 % of unprotected KBAs increase the global PA coverage to 17%. PAN refers to protected area network and KBA to Key Biodiversity Areas.

	Threatened species			**Data Deficient species**		
Area of interest (number of analysis variant used)	**mean**	**gap spp (%)**	**full spp (%)**	**mean**	**gap spp (%)**	**full spp (%)**
PAN (1)	32.5	672 (14)	302 (6.29)	30.3	681 (29.28)	238 (10.23)
PAN and top 10 % of unprotected KBAs (2)	50.3	162 (3.38)	775 (16.15)	36.7	562 (24.16)	320 (13.76)
PAN and all KBAs (2)	54.3	124 (2.58)	828 (17.25)	42.7	463 (19.91)	372 (15.99)
PAN and unrestricted expansion areas (1) (same size with top 10 % of unprotected KBAs)	62.3	26 (0.54)	1324 (27.58)	38.2	515 (22.14)	332 (14.27)
PAN, KBAs and priority areas outside KBAs (3)	82.3	2 (0.04)	2445 (50.95)	86.6	0 (0)	1484 (63.8)

3.2. Priority areas for PA expansion within unprotected KBAs

We found that the highest ranking unprotected KBAs would be very effective in improving the representation of species ranges within the PA network (Fig. A3). Zonation produces a continuous ranking of the priority areas, but from here on, we focus on 10% of the highest ranking unprotected KBAs, which are referred to as top priority KBAs. The arbitrary 10% cut off value was chosen for communication purposes, but it also falls to the period in the priority ranking where the benefit of including new areas to the priority set, measured as species ranges covered, decreases quickly (Fig A3). The exact priority ranking of all unprotected KBAs is provided in a supplementary file (supplementary file B). The results of the analysis (2) identifying the priority KBAs for PA expansion show that by protecting the top priority KBAs (0.36% of terrestrial area) it is possible to increase the mean coverage of ranges of threatened species by 17.8 percentage points while decreasing the number of gap species from 672 (14.00%) to 162 (3.38%) and increasing the number of species fully covered from 302 (6.29%) to 775 (16.15%). As expected, the mean coverage of threatened species ranges was higher for the unconstrained solution than for the one limited to using KBAs as expansions (Table 2).

Priority KBAs for PA network expansion consisted of 1,882 individual sites, with median size of 76.2 km^2, which is close to the average size of the unprotected KBA sites (median 82.9 km^2, Kruskal-Wallis test, df = 1, $p = 0.09$) (See Fig A5 for a breakdown of the size distribution) and considerably larger than average size of protected areas (median 0.5 km^2, Kruskal-Wallis test, df = 1, $p < 0.001$). Most priority KBAs were located at lower latitudes (Fig. 2), especially in Central America, the Amazonian Andes, Eastern Madagascar, and Southeast Asia (Fig. 2). Priority KBAs had, on average, more establishment criteria attached to them (2.49 criteria / area) compared to the other unprotected KBAs (1.84 criteria / area). Criteria focusing on species rarity were more common in the priority sites than among the other unprotected KBAs (Table 3).

Table 3: *Percentage of KBAs with different establishment criteria. Different groups refer to priority KBAs, all unprotected KBAs and all KBAs. The sum of the proportions within the groups is higher than one because single KBA can be established based on multiple different criteria. The criteria refer to the reasons why the KBA was established for as mentioned in the KBA dataset (KBA Partnership, 2016): CR/EN = Important for Critically endangered or Endangered species, VU = Important for Vulnerable species, endemic = Important for endemic species, migratory birds or congregations = areas important for bird migration or other species seasonal congregations, other = mixture of all other criteria (see for example IUCN 2016a for full description).*

criteria	**priority**	**unprotected**	**all**
CR/EN	0.71	0.38	0.34
VU	0.63	0.43	0.40
endemic	0.73	0.31	0.28
migratory birds –	0.15	0.33	0.33

congregations			
other	0.26	0.39	0.42

Median HII within the priority KBAs was 18.20 (theoretical maximum 72), which is slightly lower than the median of all unprotected KBAs (19.30, Kruskal-Wallis test, df = 1, p < 0.001). Specifically, 25 priority KBAs without any protection had mean HII value ranking among the highest 5% of all unprotected KBAs (HII > 40.20) and 27 among the lowest 5% (HII < 5). Figure 2A shows priority KBAs with the highest HII as red dots and those with the lowest HII in as green dots (See tables A3 and A4 for more information about these KBAs).

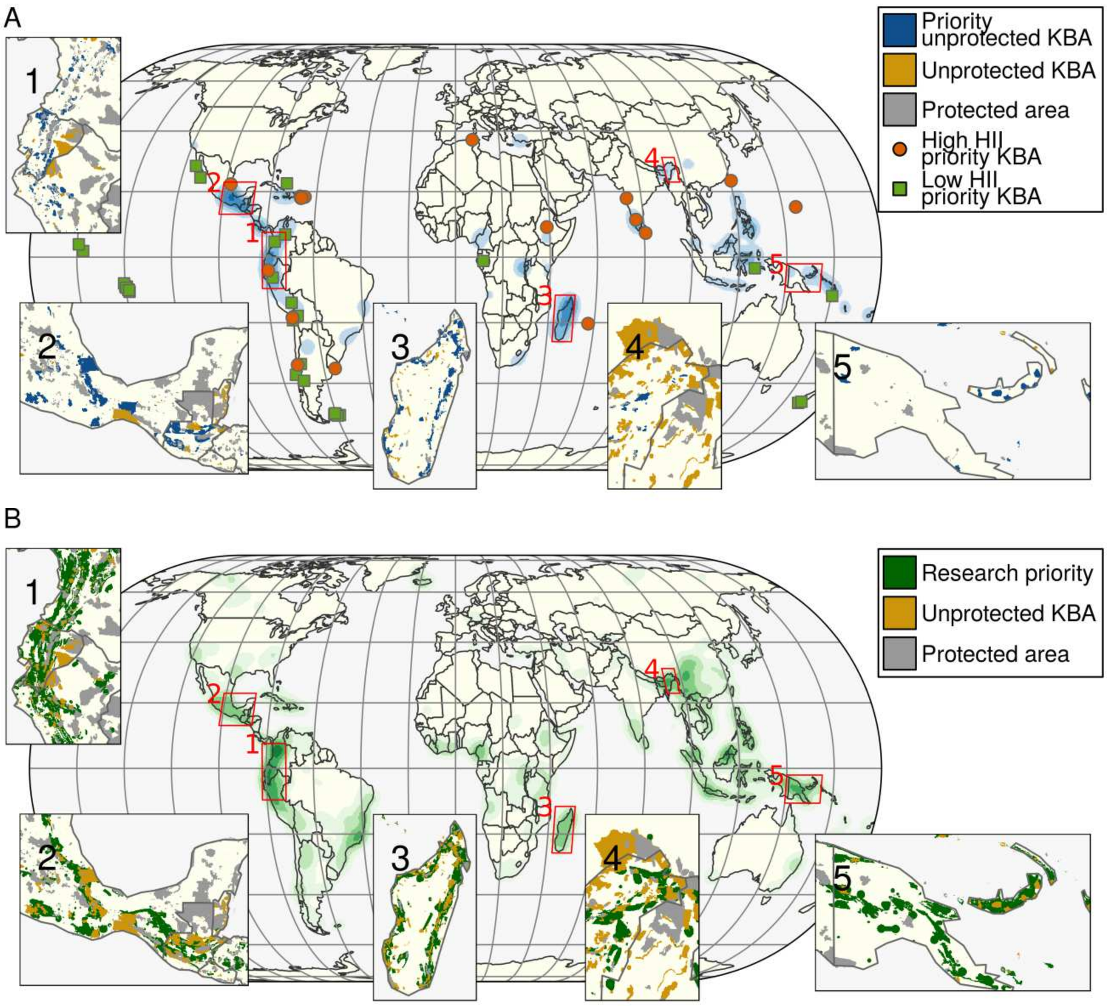

Fig. 2: Priority KBAs and priority areas outside KBAs identified in the analysis. The main map in panel A highlights the areas that contain a high density of priority Key Biodiversity Areas (KBAs) for protected area expansion based on threatened species ranges. Panel A also shows priority KBAs with high (> 40.20) and low (< 5) human influence index (HII) as red and green dots respectively. Panel B highlights locations with a high density of outside KBA network priority areas that are potential areas for effective protected area and KBA network expansion. Inset maps show detailed arrangements of priority KBAs, priority areas outside KBAs, unprotected KBAs and protected areas in selected locations. A full resolution map of priority KBAs is provided in the supplementary material (supplementary file C: analysis outputs).

3.3. Priority areas outside the KBA network

The distribution of priority areas outside the KBA network was similar to the pattern of KBA priorities (Fig. 2): the Amazonian Andes, the Atlantic coastal forest in Brazil, Western Africa, continental Southeast Asia and Papua New Guinea were highlighted as areas with highest potential for KBA and PA network expansion. If placed under conservation management, the these areas would increase the coverage of threatened species ranges by an additional 28 percentage points compared to PAs and KBAs alone (from 54.3% to 82.3%) and leave only 2 species without any conservation coverage (Table 2). The priority areas outside the KBA network also overlap with ranges of all Data Deficient species with a very high mean coverage of 86.6%. Accounting for Data Deficient species and GBIF observations in the analysis did not alter the general global priority pattern (Fig. A2). Its effect on representation of threatened species was also negligible, but representation of Data Deficient species ranges and GBIF observations were increased drastically (Table A2).

Table 4 shows that compared to other species groups amphibians might benefit relatively more from grid based prioritization that allows selecting sites also outside the unprotected KBAs (analysis 1). This can be noted from a relatively larger increase in the representation of amphibian species in the grid based PA expansion as compared to the analysis that is restricted to unprotected KBAs (analysis 2). On average, amphibian ranges are covered better than other species groups in both analyses and in protected areas. This is probably caused by relatively small range sizes of amphibians (median 39600 km^2) which are easier to cover in the prioritization analyses compared to larger ranges of mammals and birds (median 675 000 km^2 855 000 km^2 respectively).

Table 4: Mean percentage of species ranges covered by protected areas and priority sets identified by grid-based (analysis 1 in table 1) and KBA-based analyses (analysis 2 in table 1). Priority sets refer to 10% highest ranking KBAs and similar area of highest ranking grid cells. Increase in the mean representation of species ranges in the free approach compared to the KBA based approach is calculated as: free priority / priority KBAs x 100.

Species group	Coverage of ranges (mean %)			Increase in representation of the free approach compared to the KBA based approach (%)
	PAs	priority KBAs	free priority	
Amphibians	35	23	42	186
Birds	29	15	22	145
Mammals	30	13	20	151

3.4. Country responsibility of the priority areas

Priority unprotected KBAs were found in 118 (47%) countries. The priority KBAs were highly concentrated, so that six countries, Ecuador, Indonesia, Madagascar, Mexico, Peru and Philippines, alone covered 45.2 % of all priority KBA surface. In addition, 73.3% of the priority KBA surface areas was located in middle income countries (n = 102). Low income countries (n = 34) covered 19.4%, while high income countries (n = 79) covered 7.1% of the total surface area of priority KBAs. High correlation between the proportion of priority KBAs with proportion of priorities outside KBAs (identified with analysis 3, Pearson $r = 0.79$, $p < 0.001$) and unrestricted priorities (identified with analysis 1, Pearson $r = 0.93$, $p < 0.001$), suggest that same countries bear high responsibility of the overall global conservation priorities despite the identification method. Full data is provided as supplementary material (Table A5). The fact that representation of data deficient species and GBIF observations is improved without changes in the global priority pattern suggests that the improvement is caused by local level shift in the priority pattern.

4. Discussion

4.1. Unprotected KBA priorities for global protected area network expansion

Recent analyses of global conservation priorities have reported high potential for increasing coverage of species ranges with small additions to the PA network (Butchart et al., 2015, Pouzols et al., 2014, Venter et al., 2014). These analyses have successfully directed attention towards areas where protection would benefit global biodiversity the most. Nevertheless, as the analyses have been mostly based on large grid cells or ecoregions as planning units, the priority areas could not necessarily be protected as such. Deciding about which particular areas to protect within the identified priority areas would require additional knowledge about local circumstances. Selecting areas for protection within the priority sites could lead to unexpected outcomes because the areas that are important for biodiversity might not be available for conservation purposes or the priority grid cells might not alone be suitable for sustaining important ecological processes (Hurlbert & Jetz, 2007).

Our results show that large gains (18 percentage points) in species representation could also be achieved with very limited area if the PA network is expanded to priority KBAs (0.36% of land area, Table 2), which clearly are units fit for conservation. To meet the 17% area coverage target, three-quarters of the unprotected KBAs should be protected. This would further increase conservation coverage of threatened species, although not as effectively as selection that combines unprotected KBAs and freely selected areas (Table 2). It is good to remember that at the same time as countries are pursuing to reach the PA coverage targets set by the CBD, many PAs are lacking funds for proper management (Waldron et al., 2017). To truly slow down the biodiversity crisis, resources should also be targeted to improving the management of existing PA network (Waldron et al., 2017).

Using global conservation priorities to inform local conservation action is challenging. However, using unprotected KBAs as planning units, as we did here, can help reduce the gap between global priorities and local level conservation actions. We provide a list of priority KBAs as a supplementary table (see supplementary table A3 for the top priority KBAs under high pressure and supplementary file B for full list of unprotected KBAs) and hope that it could be used to draw attention to those unprotected KBAs that are the most valuable from the point of view of global conservation priorities. Our results also demonstrate that it is possible to do this without compromising overall representation of biodiversity.

The global pattern of priority KBAs agrees with priorities identified in previous global analyses (Butchart et al., 2015; Pouzols et al., 2014; Venter et al., 2014) and with the priority pattern outside KBAs. This is caused by the underlying richness pattern of restricted range vertebrates (Jenkins et al., 2013), which strongly drives all global conservation prioritization analyses that account for species ranges. The fact that most of the global priority areas for conservation are situated in the global south where funds for conservation might be scarce (middle or low income countries), sets additional challenge for moving from plans to implementation. Therefore mobilization of resources at the global level, which is the focus of Aichi target 20 (UNEP-CBD, 2010), should also have high importance for post 2020 conservation plans.

Nevertheless, even within regions with the highest density of global priority KBAs and priority areas outside KBAs, there were individual KBAs that were not included in the priority KBA set, indicating variation in the importance of KBAs at the regional level (Fig. 2). The areas that are ranked high compared to the surrounding areas are likely to contain small ranged species that cannot be covered anywhere else, whereas areas ranking lower than their surrounding areas might only contain species that are already well covered by PAs or other KBAs.

4.2. Priority areas outside KBAs needed to cover all species

The aim of the grid-based priority analysis of areas outside the KBA network was to focus attention to sites that might well be valuable for improving the complementarity of the global PA and KBA networks, but that simply cannot be reached with an analysis that is restricted to KBAs only. Compared to the unprotected KBAs, which are delineated for conservation, these sites cannot be assumed to be suitable for conservation as such. The availability of these sites for conservation and possible delineation of new PAs should be based on ground surveys, with site level information about actual species occurrences, habitat quality, costs and social factors. (Margules & Pressey, 2000).

Typically countries with many priority KBAs had also many priority areas outside KBAs. These countries have high species diversity and many species with very restricted ranges. Of all countries, Madagascar had the largest share of the global priority KBA surface area within its borders (12%) (Table A5). It also covered 4% of the total global surface area of the priority areas outside the KBAs (the eight highest of all countries). Indonesia had the largest share of surface area of global priority areas outside KBAs (10%) and third highest share of global priority KBA surface area (8%) (Table A5). Some countries like Fiji had most of its surface area assigned to either priority KBAs or priority area outside KBAs, but responsibility of the overall global priority remained small due to the small size of the country.

One of the most notable differences between the prioritization approaches was the low density of top priority KBAs combined with high priorities outside KBAs in mainland Papua New Guinea, which is commonly recognized as a global conservation hotspot (Jenkins et al., 2013). This area has very few PAs and few unprotected KBAs available for selection, increasing its importance as an area for establishing new PAs or KBAs. On the other hand, some large countries like China, had considerably high responsibility of the priority areas outside KBAs, but at the same time, although unprotected KBAs would be available, relatively few priority KBAs (Table A5). This could indicate that there are many threatened species that are missed by both PA and KBA network. In contrast, some countries, like

Guatemala, had considerably lower overall responsibility of the priority areas outside KBA network than inside KBA network (Fig. 2), suggesting that comparatively many species in that area are already well covered either by KBAs or the PA network.

KBA standard suggest quantitative analyses as a one option to identify new KBA sites (IUCN, 2016a). Therefore, the priority sites identified here could also be used to indicate possible areas for KBA expansion. Nevertheless, it should be noted that because our priority analyses were based on species data only, they cover only one part of KBA criteria (IUCN, 2016a) and thus their usability for KBA expansion is limited to identifying sites that are valuable for threatened species (KBA criteria A1, IUCN, 2016a). Priority analyses that could account for other criteria such as, migration and ecosystems would be needed to improve subsequent analyses for KBA expansions.

The current KBA network is strongly based on the Important Bird Areas that have also functioned as an inspiration for the whole KBA concept (Eken et al., 2004). Although KBAs are currently identified with a broader biodiversity focus (IUCN, 2016a.), due to historical reasons, birds can still be expected to be better covered by the network. This might lead to a situation where prioritization that is based on the KBAs might favor bird species. In our analysis there are no strong signs of this, as is shown by the relative large cover of other species groups by the priority KBAs and KBAs as a whole (table 4). On the other hand, compared to birds and mammals, amphibians would benefit more by not restricting the prioritization to KBAs. This is because a large number of small ranged amphibians that are not covered by the KBA network. Although the differences are not large, one should be cautious when using KBAs for conservation prioritization of species groups that have not been at the focus of the KBA identification work.

Priority areas outside the KBA network are especially important for Data Deficient species, many of which are missed by priority KBAs (Table 2). This is not surprising, because the KBA standard particularly emphasizes the importance of confirmed knowledge about species occurrences (IUCN, 2016a). Because Data Deficient species might well be rare and have restricted ranges (Bland et al., 2015; Trindade-Filho et al., 2012) and because it was possible to account for them without compromising representation of endangered species (Table A.2), including them in analyses for expanding PAs outside the KBA network is the safest bet.

We also found that GBIF species observations can be accounted for in the priority analyses without notable loss in coverage of species ranges (Table A.2). Because there were only few observations per species and because GBIF observations are known to be taxonomically and spatially biased (Meyer et al., 2015), global priority setting cannot rely solely on them. For the same reasons, building reliable species distribution models at global scale might be challenging (van Proosdij, 2015). Nevertheless, we believe that species observations can safely be used to identify areas with higher confidence of species presence in a analyses that are based on species ranges only.

4.3. Global analyses are restricted by data availability

Our analysis aimed to efficiently increase the coverage of threatened terrestrial vertebrate species. However it did not account for other ecological factors influencing the KBA status of an area (IUCN, 2016a). This is reflected strongly in the higher proportion of species occurrence-based establishment criteria within the present priority KBAs. This observation is consistent with Di Marco et al. (2016), who found that higher ecological irreplaceability of KBAs was associated with presence and number of restricted-range species. Other establishment criteria such as importance for species migration or importance for species that were not accounted for in this analysis can partly explain why some KBA seems to contribute only little to the global conservation coverage of species ranges in the present analysis. Further, our analyses give highest value for sites that are important for many species at the same time. In this type of approach, areas that might be critically important for some individual species, but are otherwise species poor, might not appear as high priority. It is important to note that these areas might still be valuable for conservation and need protection, although they are not the areas that are the most effective jn enhancing the representativeness of the global protected are network.

As a data-driven process, the outputs of conservation prioritization analyses should be interpreted according to understanding about underlying data and methods. Firstly, results only apply to taxa included in analysis, in this case threatened and data deficient terrestrial birds, mammals and amphibians. The effectiveness of the priority areas in covering other taxa should be treated cautiously since several meta-analyses have reported low performance of between-taxa surrogates (de Morais et al., 2018, Westgate et al., 2014). Thus, species groups with limited distribution information at global level, such as invertebrates, could be given special attention when new KBAs or PAs are established based on locally available data. On the other hand, Surrogates are also likely to work better in prioritization studies with broad extent (Lamoreux et al., 2006, Westgate et al. 2014) and large number of species (Kujala et al., 2018) like this one. Nevertheless even at the global scale, adding completely new taxa with many species is likely to cause some shifts in the locations of the priority areas (Roll et al., 2017). Secondly, although being best available, the range maps are known to have limitations as biological data (Di Marco et al., 2017), although with large data sets effects of problems with individual layers are strongly reduced (Kujala et al., 2018). It has also been shown that although the importance of site for individual species might be difficult to determine from the range maps the importance for biodiversity in general can be inferred more robustly (Maréchaux et al., 2016). Our attempts to use GBIF data to improve the prioritization also works towards improving the analyses based on the range maps, but as there are only few observations available it is nowhere near solving the problem. Thirdly, other factors like cost and threats can have large effect to the priority pattern (Carwardine et al., 2008). We decided not to account for costs or threats directly in our analyses, because we wanted to follow the approach taken by the KBA standard and focus purely on identifying sites that are important for species persistence at the global level (IUCN, 2016a). Therefore, although our prioritization analyses are effective in terms of area and vertebrate species representation, it might neither be the cheapest solution nor necessarily identify areas having highest urgency for protection of other higher taxa.

Instead of inputting threat data directly to the prioritization analysis itself, we highlighted the biodiversity priority sites with highest levels of human influence within their borders as areas that might require action most urgently (Di Minin et al. 2019). KBAs with both high and low HII were evenly represented in the set of priority sites making it possible to focus on sites with high or low pressure (Fig. A6). KBAs with high human influence might need protection most urgently, but at the same time these sites might be more expensive to protect because they area also important for human activities. As a comparison, Venter et al 2014 used agricultural opportunity cost and Butchart et al (2015) human population density as a cost layer in their prioritization analyses. These factors are likely to be correlated with HII and therefore drive the priority areas away from the areas with highest pressures. Our view is that, because especially at the global scale, it might be difficult to say whether the areas with high pressure and high cost should be preferred or avoided, it is safest to simply identify areas with highest value for biodiversity and let the end users to decide which sites to prefer.

Our results reflect the priority rank of the sites especially at the time of the analysis. When new KBAs and PAs are established or new biological data becomes available the priority pattern will be affected. For example if protection of some species is improved in one location, the priority ranking of areas containing that species elsewhere is likely to be reduced. Therefore, although the overall global priority pattern is rather robust against small changes, if the ranking is used for local level decision making, the analysis should be update whenever there are large changes to the input data.

4.4. Using KBAs improves the robustness of the prioritization

Using KBAs as selection units sets additional constraints to the prioritization analyses (Moilanen et al., 2009), which inevitably reduces their theoretical performance compared to a grid-based analysis (Table 2). The reason for this is that even the high priority KBAs will include some lower priority areas, and some areas with high value are located outside the KBA network. Despite the lower theoretical performance of the KBA based solution, it might be more effective for guiding the expansion of the global PA network in practice. This is because the priority areas identified in the pixel-based solutions are likely to contain areas that are not suitable for protection due to factors that were not accounted for in the analysis. For example information on current land use, land ownership (Di Minin et al., 2017) and local ecological processes (Pressey et al., 2007) are important for establishing protected areas, but cannot be accounted for directly in global scale conservation prioritization analyses. Further, the pixel-based priority areas might be too small and have shapes that are not suitable for effective management of protected areas.

On the other hand, based on the IUCN standards, the KBAs, and thus also the priority KBAs, should be delineated in a way that allows effective management and important ecological processes to be sustained within the areas (IUCN, 2016a). Detailed local level knowledge about factors influencing the suitability of areas for protection can also be accounted for already when the KBAs are delineated (IUCN, 2016a), making the priority KBAs more likely to be directly suitable for protection. KBAs are shown to represent local biodiversity better than expected compared to the surrounding landscape (Di Marco et al., 2016). This is likely to further improve the actual performance of the KBA based solution by reducing commission errors that are inherent for the global scale species data (Di Marco et al., 2017). Finally, in addition to conservation value identified in this analysis, the priority KBAs are already identified to be crucial for global biodiversity by the KBA method making them a double priority and thus prime candidates for protection.

Nevertheless, it is important to notice that some species are totally missed by the current KBA and PA networks (Table 2). To improve the coverage of these species, the priority KBA approach should be supplemented with new KBAs and PAs that are established in the priority areas outside of the KBA network (fig 2). Compared to the areas identified in the priority KBA analysis, more field studies are needed in these areas to confirm the presence of the species and to collect information about local circumstances before any on-the-ground action can be taken.

5. Conclusions

Our objective was to rank KBAs in terms of how well they would complement the current PA network and thus work as an effective expansion for it. Every KBA is by definition important for biodiversity, and continues to be so, whether or not it was included in the priority sets identified here. We are not suggesting that protection is the only solution for safeguarding the conservation value of KBAs. In many cases, the biodiversity value of a KBA could well be maintained with other conservation actions (IUCN, 2016a). Nevertheless, most of the top priority KBAs and priority areas outside KBAs are located in regions where pressures on biodiversity are expected to intensify (Tilman et al., 2017). Therefore, strengthening the conservation status of these areas that overlap with the ranges of many globally threatened species might be a worthwhile investment for the future.

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7. Data and data manipulation

The code for data manipulation, analysis and production of this document is provided in https://github.com/PKullberg/Priorities_for_KBA_research_and_protection[*the link to the final version will be made public after publication*]. Zonation software is available from www.helsinki.fi/en/researchgroups/digital-geography-lab/software-developed-in-cbig. All relevant data is derived from published sources indicated by the citations in the methods section.

8. Supplementary files

Supplementary file A: additional figures and tables (https://drive.google.com/file/d/17gCMWhXQC2uMaINLH2j_1Bd0-nr0SqCQ/view?usp=sharing).

Supplementary file B: full list of KBAs, available at https://drive.google.com/file/d/1wd7dbb8LkbCG1V1wqHWz4wd6513i5_yR/view?usp=sharing *(This will be moved to a permanent repository after acceptance)*.

Supplementary file C: The result files of the priority analyses including the detailed priority maps can be downloaded from: https://drive.google.com/file/d/1j17jb_rh3EEFSYim7MF1lIRfbejBJrLR/view?usp=sharing. *(This will be moved to a permanent repository after acceptance)*

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Highlights

1. We prioritize unprotected KBAs for effective expansion of the global PA network
2. Analysis is based on terrestrial vertebrate ranges and uses KBAs as planning units
3. Priority KBAs covered biodiversity broadly but some species were missed
4. Restricting expansion only to KBAs lowers the representation of biodiversity
5. Priority KBAs with few critical additions are a good complement for the PA network